Behavioral Adaptation of the Giant Clam *Tridacna maxima* to the Presence of Grazing Fishes

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(Plates 2 and 3; 3 Text figures; 1 Map)

INTRODUCTION

Among the spectacular molluscan groups from the tropical Indo-West-Pacific zoogeographical region are the giant clams, or Tridacnidae, a family of several, often variable species not all of which attain gigantic proportions. The colorful mantle and the exposed nature typical of the group make them conspicuous members of the reef fauna (Plate 2, Figure 1). Byssal attachment to a coral substratum is usual, but large individuals of certain species lie unattached upon the bottom of the sea (Yonge, 1936).

As in the majority of bivalves, the general habitus of the tridacnids is one in which the siphonal mantle lobes are upwardly directed. In this family, however, the posterior portions of the body far exceed the remaining portions in relative size. These relative proportional differences are suggested by the extent of comparable regions outlined on the lateral surfaces of the shells of *Tridacna* and *Clinocardium* (Text figure 1). The siphonal mantle lobes extend over the margins of shell regions *b* and *c*, between the end of the pedal gape (PG) and the end of the ligament (PL). As illustrated in Plate 3, Figures 1 and 2, the hypertrophied mantle lobes of *Tridacna* are completely exposed to the surrounding sea. While one might not be surprised that defensive mechanisms exist in correlation with this kind of sessile and conspicuously epibenthic habitus, the Tridacnidae have been believed insensitive to all but very considerable mechanical stimuli (Yonge, 1936, p. 304).

The present paper relates previously undescribed aspects of behavioral activity of *Tridacna* and draws conclusions concerning its adaptational significance.

Tridacna AT FANNING ISLAND

As a participant in the Fanning Island Expedition, 1963, I had opportunity to study living *Tridacna maxima* Röding, 1798, the sole, but variable species of the family found on the atoll, which lies about 1000 miles south of the Hawaiian Islands and on the eastern boundary of the geographical range of the Tridacnidae. In a previous paper (Stasek, 1962) this species was referred to *T. elongata* Lamarck, 1819, but Dr. Joseph Rosewater, USNM, (in correspondence) considers the present name the correct designation. The accompanying map records the collecting localities at which living specimens were found. *Tridacna* occurring about the unnumbered "Transect" locality in approximately 4 meters of water on the outer reef slope were exceptionally large for the species (Plate 3, Figures 1 and 2). The largest collected specimen measured 417 mm in greatest dimension. SCUBA proved necessary for observations in this locality. Snorkle and face plate were sufficient in localities within the lagoon, and *Tridacna* could be collected by wading in localities 7, 14, and parts of 19.

While *Tridacna maxima* is characteristically byssally attached to a solid coral substratum, often within shallow or deep depressions of its own making, many specimens in Collecting Locality No. 18 were found in about 3 - 5 meters of water on a coral sand bottom. This locality was typified by a series of large offshore, steep-sided knolls composed mainly of mixed coral genera (*Porites, Acropora,* etc.). The knolls, estimated to be a maximum of 2.5 meters high, were isolated one from the other by relatively narrow channels, the floors of which were coral sand. It was on this sand that the *Tridacna* lay free. Each free *Tridacna* possessed a strong byssus fixed to a small piece of broken coral skeleton, usually *Acropora.*

Living, uninjured specimens from Collecting Locality No. 5, where *Tridacna* was common in water less than 2 meters deep, were kept in small plastic aquaria or were transferred to Danger Point Pool (see map) for observations.

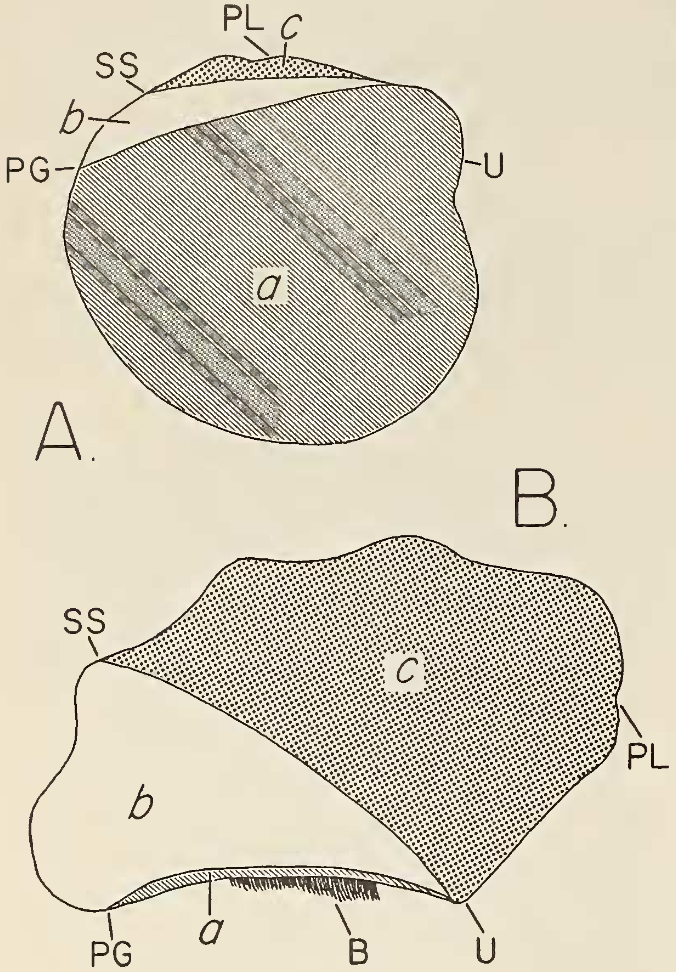

Figure 1:

Diagrams of the lateral surface of the right valve of *Clinocardium* (A) and of *Tridacna* (B). Lines drawn along radii between the umbo (U), which is greatly enrolled in *Clinocardium,* and the posterior end of the pedal gape (PG) or the siphonal septum (SS) divide each valve into three comparable, but disparately sized regions (*a, b, c*). The relative sizes of these regions are directly correlated with the degree of development of adjacent components of the mantle and body. Hence, while "locomotory regions" of the body and shell (*a*) are emphasized during growth of *Clinocardium,* the "siphonal regions" (*b* and *c*) disproportionately enlarge in *Tridacna,* which is attached by a byssus (B). PL, posterior end of ligament.

Large series of subfossil *Tridacna* and other mollusks were found lying on the soil surface near the middle of the Transect Line.

All reactions reported below were observed to occur in the field as well as under laboratory conditions.

OBSERVATIONS

Reactions to mechanical stimulation. A child, gently prodding the exposed mantle lobes of a *Tridacna* contained in a small aquarium, accidentally discovered a significant fact. Namely, that regardless where he stood relative to the clam, the resulting stream of water shot from the exhalant aperture to a distance of about two-thirds of a meter beyond the rim of the aquarium invariably got him wet if he prodded that part of the mantle nearest him. That is, upon stimulation, the stationary clam obviously had the ability to orient the stream of exhalant water towards the region of mechanical irritation of the mantle. Following this discovery, responses of expanded *Tridacna* to probing were observed to be as follows:

In an expanded, undisturbed position the exhalant aperture, which lies at the end of a short cone, is directed upwardly away from the inhalant aperture (Plate 3, Figure 3; Text figure 3, EA). When a limited region of a mantle lobe was gently probed one to several times with a blunt wire, there resulted a withdrawal of the single mantle expansion touched, the exhalant aperture remaining open. In this simple response the edge of the mantle withdrew approximately 3 or 4 mm from the shell margins. Continued stimulation of the mantle expansion, even if gentle, resulted in an overlapping and infolding of the lateral lips of the exhalant cone, as depicted in Text figure 2. The exhalant aperture was closed by this process.

Concurrently with the infolding of its lips, the exhalant cone rapidly elongated with the closed aperture directed toward the area being probed, and the entire mantle margins of both right and left sides retracted nearly out of sight between the gaping borders of the shell. As the cone expanded, its walls became obviously thinner. A violent closure of the shell then drove a powerful current of water from the exhalant aperture toward the region of stimulation. The aperture was apparently opened by muscular relaxation and by sudden increase in internal water pressure. Plate 3, Figures 4 and 5 illustrate the exhalant cone photographed in the process of "aiming."

Sand sprinkled between the mantle lobes did not result in directed movement of the exhalant cone or in spurting from it. Large pieces of coral gravel placed in that position did result in this behavior. Such gravel was usually cleared away at once, but often 2 or 3 attempts were necessary to accomplish this clearance.

While the lips of the exhalant aperture infolded and the entire cone elongated just prior to a spurting reaction, the margins of the large inhalant aperture (Plate 3, Figure 3; Text figure 3, IA) were slightly infolded and pulled together, probably by contraction of longitudinal mantle muscles in the rims of the aperture.

Plate 2

Figure 1: *Tridacna, in situ,* as seen from above. Photo taken at the isolated intertidal locality in Rapa Passage.

Figure 2: Small *Tridacna* with mantle lobes expanded and showing spots of blue structural pigmentation; groups of zooxanthellae scattered generally in the tissues; a marginal row of dark spots, each indicating location of a "hyaline organ"; and a regenerated notch of mantle containing "hyaline organs". Specimen from Palmyra Island, Line Islands. Photo by S. A. Wainwright.

Figure 3: Roving school of surgeon fish (Manini) in Danger Point Pool.

Figure 1

Figure 2

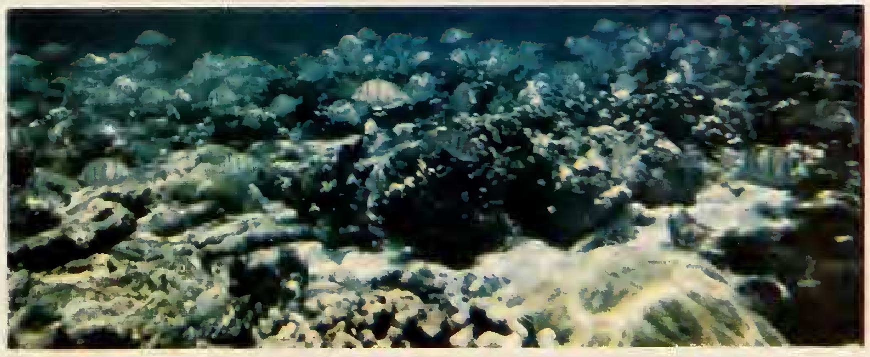

Figure 3

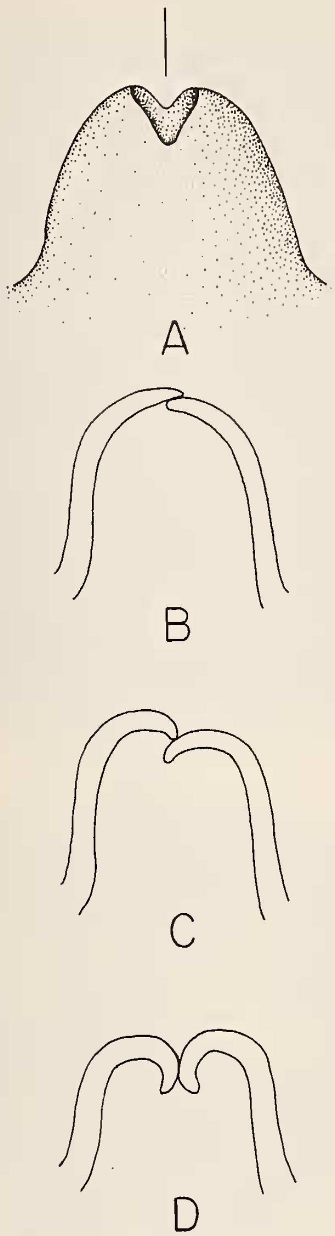

Figure 2:

Tridacna. A Exhalant cone seen three-dimensionally, aperture open. Sagittal plane, indicated by line above aperture, is at right angles to plane of paper. **B - D** The cone drawn as though sectioned perpendicularly to the sagittal plane and showing three stages of the overlapping-infolding process.

Responses to probing differed according to the part of the mantle stimulated. If the mantle lobes were probed anywhere between the upper margin of the inhalant aperture and the end of the ligament, the exhalant cone became active and reacted as described above.

Stimulation of the lip margins of the exhalant aperture resulted in a violent and upwardly directed spurt of water.

If the mantle lobes bordering the inhalant aperture were probed, water was ejected in a strong, gushing fashion from that aperture only. The exhalant aperture infolded and closed, but the cone was not directed toward the point of irritation.

Water ejected from the inhalant aperture when the mantle lobes adjacent to it were stimulated was directed toward the side of stimulation. This directed response occurred because of a differential retraction, or lowering of either the right or left margin of the aperture, depending upon which side was probed. This retraction resulted in a deflection of the stream of water from the higher toward the lower side of the aperture.

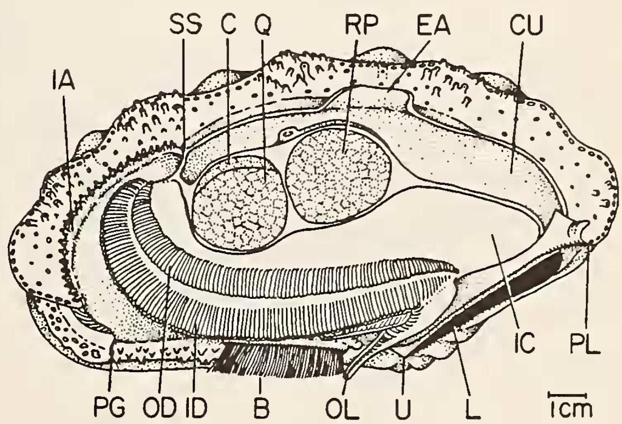

Figure 3:

Tridacna maxima. Organs of the mantle cavity as seen from the right side. Right valve and mantle lobe have been removed (modified from Stasek, 1962).

B - byssus emerging from foot; C - catch portion of adductor muscle; CU - supra-branchial cul-de-sac; EA - exhalant aperture; IA - inhalant aperture; IC - extension of infra-branchial chamber; ID - inner demibranch of ctenidium; L - ligament; OD - outer demibranch of ctenidium; OL - outer labial palp lamella; PG - posterior end of pedal gape; PL - point at which right and left mantle lobes fuse at end of ligament; Q - quick portion of adductor muscle; RP - posterior pedal retractor muscle (area of insertion on right valve); SS - siphonal septum dividing infra- and supra-branchial chambers; U - umbo.

Stimulation of the minutely tentacled border of the inhalant opening resulted in a violent spurt of water directed straight out through the aperture.

Thus there are two zones of the hypertrophied mantle lobes, an extensive "exhalant zone" (Text figure 3,SS-PL)